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THE ORIGIN AND RELATIONSHIPS OF THE ARAUCARIANS. I

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Perhaps I can make the purpose of this paper clear in no better way than by quoting a sentence or two from a recent paper by JEFFREY (**42**):

> The comparative, developmental, paleobotanical, and experimental investigation of the Coniferales is likely to throw more light on the stable and sound general principles of biology than that of any other large group of animals or plants, on account of their great geological age and remarkably continuous display, both as regards external form and internal structure in the strata of the earth. . . . .
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> It is finally clear that morphologists will find it necessary in the future more and more to adopt certain general working principles, as for example in the sister sciences of chemistry and physics. If there prove on trial to be no generally applicable fundamental principles in morphology, that branch of biological science cannot be too soon cast into the outer darkness, which prevails outside the scientific view of nature.

It is doubtful whether anyone is likely to dispute the truth of the first sentence quoted above. At any rate, it is sufficiently accurate to make an examination of the various opinions concerning the origin and relationships of the araucarians well worth while. It is a conspicuous fact that among those most familiar with the facts now known regarding conifers, the most diverse opinions are strongly held. It is further to be observed that these various opinions are grounded on the different values set upon different

classes of facts. The object of this paper is to attempt to set forth the principal views and to show on what sort of evidence each rests. Having gotten at the facts, we may then inquire into the relative merits of each sort of evidence and attempt to evaluate them. If such an evaluation could be made, we might rescue the subject of morphology from the fate of being "cast into outer darkness." I am very little inclined to think that it will be possible for any one investigator to set forth the evidence in a manner to satisfy the adherents of all views, but my purpose will be served if I shall induce those more competent to take up the subject with the serious intention of determining just what principles are generally applicable, if there are any, and what are the limitations to which various sorts of evidence are subject.

In a broad way the opinions regarding the origin of the araucarians may be grouped under three heads: (1) the lycopod theory, (2) the cordaitean theory, (3) the abietinean theory. In setting forth these various theories I shall attempt to present the salient facts and opinions of a number of those who have written on the subject, but no attempt will be made to present exhaustively the facts or even the opinions of any one. It will undoubtedly happen that in choosing what seem to me the strongest evidences for the different views and the strongest objections to them, I shall be unable to escape the effects of personal bias, and still less able to choose just as the authors themselves would choose. These are objections that cannot be wholly avoided. The best I can do is to be as impartial as possible and to beg indulgence in advance for the slips that are sure to occur.

The lycopod theory

The external resemblance of certain conifers to the lycopods has attracted notice from early times. The first serious attempt that I have found to set forth the evidence for believing that Coniferales, or at least certain of them, have originated from Lycopodiales is that of POTONIÉ (**47**) in 1899. A rather free condensation of his statement of this theory and the facts on which it is based is as follows: (1) conifers, except possibly Taxaceae, are derived from "Lepidophyten"; (2) the ancestor of a cone scale was a leaf that

was at once foliar and spore bearing; (3) this foliar organ became differentiated into two parts, (*a*) a reduced spore-bearing part and (*b*) a foliar part, somewhat after the fashion of an *Ophioglossum* leaf; (4) these compound organs were aggregated into cones; (5) in the process of cone formation the foliar portion was gradually reduced and the ovuliferous (spore-bearing) portion was increased; (6) in the pine cone the spore-bearing portion is the ovuliferous scale, in *Araucaria* it is the ligule, and in many other plants ligule-like outgrowths are to be explained in the same manner (**47**, pp. 320–323). He offers the following arguments in its support: (1) it harmonizes a great variety of facts; (2) this gradual development of the ovuliferous scale and reduction of the bract is in accord with geological history, because it is only in the Abietineae that the distinction between scale and bract is comprehensible, and they are later and more specialized forms than the earlier Araucariae and Taxodiae; (3) the brachyblast theory requires us to think of the ancestral forms as having less compact strobili and with cone scales more like a leafy shoot, and this is directly opposite to the historical fact. We shall return in a later paragraph to the question of how much of this evidence is still pertinent after the presentation of the more recent views.

In 1905 CAMPBELL (**8**) stated his opinion that "as both the pollen tube and seed formation are but further developments of heterospory, it is quite conceivable that these might have arisen independently more than once. The close resemblance between the conifers and the lycopods, especially *Selaginella*, probably points to a real relationship. The strobiloid arrangement of the sporophylls, as well as the development of the prothallium and embryo, are extraordinarily similar, and it is not unreasonable to suppose that this is something more than accidental. The strong resemblance between the method of the secondary thickening of the stem in the arborescent fossil Lycopodineae, and that of the conifers, as well as the anatomy of the leaves, suggests a real affinity. It is known that some of these bore seeds, which in structure and position may very well be compared to those of typical conifers." He reaffirmed this opinion in less precise terms in 1911 (**9**).

In 1905 SEWARD and FORD (**54**) surveyed the work upon araucarians up to that time, added a considerable body of observations of their own, and discussed thoroughly the bearing of all the available facts. They came to the conclusion that the Araucariae occupy a place so remote from other conifers that they should be set off as a separate order under the name of the Araucariales. It is difficult to summarize so extensive a paper, in itself more or less a review, within the limits necessarily set on such a paper as this. However, we may summarize briefly their conclusions and indicate more or less inadequately the nature of the evidence on which they are based. So far as their discussion of affinities is concerned, the argument may be divided into three parts: (1) Araucarineae are primitive plants; (2) there are numerous grave objections to the assumption that they have originated from the Cordaitales; (3) there are significant resemblances to various living and extinct lycopods.

1. *The Araucarineae are primitive plants.*—This thesis these authors attempt to prove in two ways. They show from a review of the fossils that have been assigned to this family that it is extremely probable that fossil stems are known as far back as the Permian, and possibly the Carboniferous, both as impressions and as petrifactions, that find their closest resemblances and affinities with the present-day araucarians. Cone scales resembling those of the EUTACTA section of the genus *Araucaria* are known far back in the Jurassic, farther back in fact than those of the Abietineae. Historically, then, they argue the Araucarineae are primitive plants. To the support of their argument from the geological record they bring the testimony of comparative anatomy and morphology. They think the primitive character of the group is indicated by the gradual transition of foliage leaves to cone scales or sporophylls, by the resemblance of the two cones in some species, by the simplicity (as they attempt to prove) of the ovulate cone, by the persistent leaf traces, by the anatomical character of the leaves, by the homogeneous character of the wood without resin canals or wood parenchyma, by the multicellular male gametophyte, by the lateral distribution of the numerous archegonia, and by the similarity of the embryo cap to a root cap.

2. *A cordaitean connection does not seem probable.*—The chief arguments for this view they summarize under three heads: (*a*) the presence of hexagonal contiguous pits on the tracheal walls, (*b*) a comparatively wide transition zone from protoxylem to secondary wood, (*c*) a resemblance in the form of the leaf and in the general habit of the vegetative shoots. They are of the opinion that the first two resemblances are of little significance because of their common occurrence among paleozoic plants. They are primitive characters, but do not necessarily indicate a relationship to Cordaitales. The external form of the leaves is not specially significant, for the internal structure does not indicate a close affinity with Cordaitales, and furthermore the more ancient araucarian leaves are less like those of Cordaitales than those of certain modern species.

Having refuted the supposed arguments for the cordaitean connection, they offer certain other objections for good measure. They point out that the leaf trace of Cordaitales is double when it leaves the primary wood, while that of the Araucarineae is single. They cite several other investigators in support of their opinion that the ovulate cone is simple in structure. They recognize that a comparison can be made between the simple appearing cone scales of *Araucaria* and the apparently double structures of the Abietineae. The evidences for the duplicity of *Araucaria* must be derived second hand from the latter. The evidence for their double nature rests on the assumption that certain abnormalities, in which an ovulate scale is replaced by a foliar shoot, indicate that the cone has been derived by condensation of a branching leafy shoot whose leaves bore ovules abaxially. While this may be probable enough (they do not even commit themselves to so much) for this group, it is not considered valid evidence in the interpretation of the apparently simple cone of *Araucaria*, which they believe to be an older type and more likely to exhibit primitive structures than the Abietineae. Their contention is that in the Araucarineae there is nothing to explain. The cone is just what it appears to be. The inverted vascular supply of the ovule is a normal feature of such bundles, and the duplicity is no more than a sort of ligular excrescence, such as is common among the Lycopodiales.

The resemblance of the male gametophyte to that of Cordaitales is no more than a parallel carried over by both from the pteridophytes. In short, there are not very many resemblances between *Araucaria* and *Cordaites*, and even these are no more than an expression of a common heritage from the pteridophytic ancestors of both. From all this SEWARD and FORD conclude that the Araucarineae are too unlike Cordaitales in too many respects to make the supposition of actual relationship probable. This conclusion leads logically up to the presentation of what they believe to be evidences of real affinity with the Lycopodiales.

3. *The significant resemblances of araucarians and lycopods* appear to these authors to be numerous and important. They recognize, however, that the application of JEFFREY'S (**27, 28, 29**) well known and widely accepted division of the vascular plants into two great divisions, the Lycopsida and Pteropsida, on the ground of the presence in the latter of leaf gaps and their absence in the former, would constitute a serious objection to a derivation of any conifers from a lycopsid ancestry. They prefer rather to question the validity of his generalization, and express the opinion that the characters on which it is founded "have been estimated at too high a value as indices of affinity."

Having thus cleared the ground by attempting to show that the Araucarineae are primitive, that it is unlikely that they have been derived from the Cordaitales, and that their possession of leaf gaps does not preclude a lycopsid ancestry, they reach the really critical portion of the argument. Direct comparisons are instituted with a number of living and fossil lycopods.

In the main body of the paper they have shown to their own satisfaction that the araucarian cone is simple in structure and so "poles asunder" from that of the Abietineae or Cordaitales. This suggests the direct comparison with the ovulate cone of *Lepidocarpon*. In opposition to the view of the discoverer (**51**), they are of the opinion that it may "constitute a (possible) connecting link between the Araucariae and lycopods" and approvingly cite SCOTT'S (**53**) admission that it furnishes an excellent argument for their view. The organization of the cone, the simple sporophylls, the single median ovule, and the ligule appear to present

so close a homology as to afford strong indications of real affinity. The method of attachment of the single megasporangium by a stalk and the similar cone scales serve to form the basis of a comparison with *Spencerites* (49).

The resemblance of the microsporophylls to those of *Equisetum* is noticed, but is not held to indicate a direct relationship. Though they admit that the typical lycopod did not have its microsporangia on the dorsal side of the microsporophyll, they think they see a certain significance in the fact that the *Araucaria* type is found in *Cheirostrobus* (50), a genus that has been thought to be one of those generalized types which serve as finger-posts to the paths which evolution has followed, and which is considered to be intermediate between club mosses and horsetails (54).

These investigators assert that not only are the ovulate cones simpler and more primitive in structure than those of other conifers and more like those of paleozoic lycopods, but they are more nearly like those fossils from the Mesozoic than are those of any other group. This accords with their view; whereas, if they had been derived directly from Cordaitales or indirectly through the Abietineae, they should show some approach to the supposed leafy shoot predicated by the brachyblast theory, as the fossil history is followed backward toward the ancestral forms. They are of the opinion that no such transitional forms are known. On the contrary, they are of the opinion that the older forms show an approach to the lycopod situation in having smaller leaves and cone scales, with a gradual transition between the two organs.

They point out that the stem apex more closely resembles that of lycopods than that of ferns, though they do not attach much value to this fact. The exarch veins of the leaf may be regarded, they think, as a possible "ancestral feature which has disappeared from the vegetative stems." The leaf traces are accompanied by a group of cells in the cortex which the authors compare to the "parichnos" in lepidodendroid stems.

While they admit that there are many points of dissimilarity between araucarian stems and those of the lycopods, they do not think that any of them constitute an insuperable barrier to the derivation of the one from the other. They point out that the

scalariform tracheids of the lepidodendroid stems is paralleled by the same structures in the transitional primary wood of *Araucaria*. They do not urge this point as a strong argument, but merely point out that the presence of the two distinct types of pitting in the mature secondary wood of the two groups does not "necessarily imply separate lines of descent." The resin canals of the araucarians can be derived as well from the mucilage cells and canals of the Lepidodendreae as from those of the Cycadofilicales.

They are strongly of the opinion that the multicellular pollen grains of the araucarian alliance are very different from those of Cordaitales or any other recent seed plants. They differ from the former in the arrangement of the cells, and from the latter in the much greater development of the vegetative cells. A comparison with the microspore of *Selaginella* or *Isoetes* appears more convincing. The reduction they "connect with the substitution of siphonogamous for zoidogamous fertilization, which would demand as much space and material as possible for the production of the pollen tube."

STILES (**61**) argues that the conifers can be derived more readily from the lycopods than from the Cordaitales. His argument is divisible into two parts: (1) an attempt to show that Podocarpeae (and hence other conifers, for he holds that all have had a common origin) cannot have been derived from Cordaitales and must, therefore, have been derived from the only other(?) available source, the lycopods; and (2) a direct comparison of conifers and lycopods to show the possibility of deriving the former from the latter.

Under the first head he adduces much excellent evidence to show that the podocarps are closely related to the araucarians. He also attempts to show that the conifers are monophyletic. The next step is to show that podocarps cannot have been derived from Cordaitales, in consequence of which the other conifers are likewise excluded from such an origin. He enumerates four points which he considers sufficient to preclude the possibility of the primitive podocarps having originated from Cordaiteans: (*a*) the stem of these podocarps is no more like that of the Cordaitales than it is like

that of conifers in general; they may have derived certain resemblances from a common ancestry but are not on that account closely related; (*b*) the roots of the podocarps are not "particularly reminiscent" of those of Cordaitales; (*c*) the primitive type of leaf among the araucarian-podocarp alliance was small and narrow and provided with a single midvein and unlike the broad parallel veined leaves of the Cordaitales; (*d*) the structure of the microsporophyll of the podocarps "no more favors this view [cordaitean origin] than the three preceding pieces of evidence." It is scarcely necessary to mention that most of these objections would be equally valid as arguments against a relationship between podocarps and araucarians, a relationship which he champions vigorously, nevertheless. It seems rather unfortunate that so many of the facts known about gymnosperms may be used almost equally well to prove a variety of quite antagonistic views.

Under the direct argument, he places first the similarity of the ovulate cone of the simpler and more primitive podocarps and of the araucarians to the lycopod cone. They are, he thinks, alike in their general structure, being in both cases composed of simple sporophylls with a gradual transition to the leaves. In both each simple sporophyll bears a single median megasporangium. In both the sporangial organ is at first erect in the axil of the scale. In certain of the podocarps he sees a tendency to the development of a double structure of the cone scale analogous to that of the Abietineae.

Secondly, "the microsporophylls are also easily comparable with those of the lycopods." The presence of more than one sporangium in the conifers "is not a serious" difficulty, since septation is well known in the sporangia of lycopods. Moreover, "the shifting of the sporangia to the under side presents little difficulty to the view under consideration," since it "has certainly taken place in other cases." The other cases cited are the *possibility* of its having occurred among the ferns, and the fact that "among the Equisetales in *Palaeostachya* the *sporangiophores* are found on the upper side of the sporophyll, while in *Cingularia* the *sporangia* are below the sporophylls" (italics mine). In any case,

whether conifers have sprung from ferns or lycopods, one sort of sporangium must have migrated to the other side of the sporophyll. This is true, of course, only if one accept the author's view that the cone scales of conifers are really simple.

The presence of seeds in *Lepidocarpon* and *Miadesmia* is held to prove that "there is thus abundant evidence that the potentiality of seed production existed in this phylum as well as in the fern phylum." Any differences that exist in the vascular supply of the sporophylls between podocarps and lycopods "is to be accounted for by the greater relative importance of the ovule as compared with the sporophyll." Small, narrow, uninerved leaves are characteristic of both conifers and lycopods, but are unknown among the Cordaitales. Those podocarps and araucarians with broad parallel veined leaves are not primitive, but have derived their leaves from narrow-leaved ancestral forms.

One of the most interesting points in the argument is the attempt to show that, while a siphonostele with leaf gaps is certainly characteristic of the fern alliances, it is not necessarily limited to them. It merely represents a goal toward which vascular plants of all sorts have tended. The ferns reached it early, while the paleozoic lycopods did not quite reach it. They did actually attain the seed habit, another one of the milestones of plant evolution, but attained only to a medullated siphonostele in which nearly all the metaxylem had been obliterated and which had become broken up in some forms into separate strands. These bundles were still exarch, however, and the leaf traces did not produce leaf gaps in the stele. These would have been the next logical steps in the evolution of the lycopod stele. The inference probably is that they were actually attained by the yet unknown lycopodialean ancestors of the conifers. While admitting that the presence of bordered pits in the secondary wood of conifers is a point against the lycopod theory, he thinks that the presence of a modified sort of pit in *Sigillariopsis Decaisnei* (48, 53) shows the possibility of their development in this phylum. The double leaf trace of the Abietineae (and Araucarineae), which has been used as an argument for the cordaitean origin, he thinks is offset by the single trace of the primitive podocarps.

The conclusion is indicated by the following quotations: "To the writer the evidence seems to point . . . . to the primitiveness in the Coniferales of a type bearing female cones composed of aggregations of simple sporophylls, each sporophyll bearing a single erect axillary ovule." "This supposed primitive conifer is very suggestive of the Lycopodiales, but is not reminiscent of the Cordaitales."

It is evident from the preceding that, aside from what support may be gained by discrediting rival theories, the lycopod theory derives its greatest strength from the three following sources.

The first and strongest argument comes from the very close resemblance in form and structure of the ovulate araucarian cone to the strobilus of the lycopods. If there were no other reasons for suspecting a filicinean origin of araucarians, and there were no Abietineae with their perplexing structures, no one would, I think, even suspect that the ovulate cone is other than what it appears to be. Notwithstanding these influences most (though not all, **20, 42, 59**) investigators (**44, 61, 69, 76**) who have studied the araucarian cone have concluded that it is really simple in structure and its cone scales simple sporophylls.

Next in importance and even more difficult to dispose of is the structure of the seed and pollen tube. SEWARD and FORD have pointed out the close resemblance of the seed structure (**54**) and the writer has elsewhere (**7**) shown that these structures could easily have arisen from the condition found in *Miadesmia* and *Lepidocarpon*, but that it is exceedingly difficult to see how, and still more difficult to see why, they should have arisen from the known types of cordaitean seeds. It is easy to see how pollination of the scale instead of the nucellus would be the most probable type in plants which developed the strobiloid habit before the pollination and seed habit. But it seems hardly probable that having been in possession of the habit of depositing pollen grains in a specially prepared and protected pollen chamber in the nucellus, any group of plants would pass through a course of evolution requiring them to give up all the advantages comprised in these arrangements and to acquire an entirely new and certainly less efficient method of pollination. Considering how very little we know of the

structure of paleozoic seeds of any sort, it would be rash indeed to suppose that the known types of seeds were the only ones found among Cordaitales, and even more rash to generalize more than provisionally on the assumption that they did not possess a particular type. We do not know whether the seed habit was developed in the phylum once or more than once, much less whether it was developed before or after the organization of cones. In short, this is today a strong argument for the lycopod theory, that the discoveries of tomorrow may become an equally valid argument for the cordaitean theory.

A third group of resemblances between lycopods and conifers is presented by the leaves. The small, narrow, uninerved type of leaf so characteristic of lycopods is very common among the conifers. The arrangement in many cases is also similar. The gradual transition from leaves to sporophylls in the lycopods presents a very close resemblance to certain araucarians. Most, or perhaps all, of these resemblances, indeed, can be explained away, but that is just where their strength as evidence for this theory lies, they do have to be explained away.

On most other points the theory appears to be on the defensive. It can, to be sure, offer more or less plausible explanations and possibilities for some of the evidence that appears to be against it, but still it must explain them in some other than the obvious way to bring them into harmony with itself. The first and most serious objection in the opinion of most of its opponents appears to be the structure of the stem, more particularly the stele. Notwithstanding STILES's ingenious and convincing exposition of the evolutionary tendencies of the lycopod stele, it yet remains true that no known lycopod did attain to the possession of a mesarch or endarch siphonostele with leaf gaps. That they might have done so appears very probable, but there is yet no evidence that they actually did so, and much less that any one that could be supposed to be a form ancestral to the conifers had even nearly approached it. The same sort of objections apply with even greater force to the attempts to explain the origin of the staminate cone structures. It is admitted by most botanists that septation has probably occurred in certain lycopod sporangia. It may even be

admitted that a shifting of sporangia from one surface of the sporophyll has occurred in some pteridophytes. Again, there is no evidence that they have occurred in any lycopod that can by any possibility serve as a starting-point for modern conifers.

I have indicated above what seem to me to be the most fundamental objections to the theory, namely, that the individual comparisons which can be made between conifers and lycopods must be made with plants of the latter phylum which are admittedly very remotely related to one another. No single lycopod is known that combines within itself any very considerable number of resemblances to the conifers. In a later paragraph I shall return to the attempt to evaluate evidence of this sort. It is an interesting fact that practically all the evidence for this theory is derived from the comparative morphology of adult plants. The two conspicuous exceptions are (1) STILES'S comparison of the erect axillary mature megasporangium of the lycopods with the position of the very young ovule of the podocarps, which is also erect and axillary, but which may later be inverted and carried out and away from the axis by the growth of the base of the sporophyll; and (2) his argument that the primitive leaf in the conifers was small, narrow, and uninerved, because many conifers have juvenile foliage of this sort.

The cordaitean theory

The majority of writers have held that conifers are ultimately to be derived from the Cordaitales. SCOTT (**53**), OLIVER (**45**), WORSDELL (**77, 78**), COULTER and CHAMBERLAIN (**16**), JEFFREY (**29, 42**), THOMSON (**70, 73**), and many others have brought forward much convincing evidence in support of this view. Although these authors agree in general as to the ultimate origin of all conifers from a common stock, there is considerable diversity of opinion as to the relationship of the tribes. In the present paper we shall consider these divergent views only so far as they pertain to the origin and relationship of the araucarians. There is a prevailing opinion that this tribe is either the primitive basal group of conifers or constitutes an independent line by itself. Opposed to this view is that of JEFFREY and his students, who have presented much evidence to show that the Abietineae are the oldest and most

primitive group, and that the araucarians have been derived from them.

The first view finds its support in (1) the many close resemblances between the modern araucarians and the paleozoic cordaiteans; (2) the apparently greater geological age of the Araucarineae; and (3) transitional forms of the Triassic and Cretaceous, which appear to become more like the Abietineae from the earliest to the later ones.

The second view does not deny the similarities pointed out as supporting the previous view, but in view of other sorts of evidence believes them to have been secondarily acquired. It does not necessarily deny that they are indications of relationship, but merely that they do not indicate direct and immediate relationship. It derives most of its positive support from (*a*) vestigial structures, (*b*) recapitulation phenomena in seedling and young wood, (*c*) traumatic responses.

Since the supporters of the lycopod theory have chosen the araucarians as the tribe most favorable to their contention, the views of their opponents can be best set forth, perhaps, by marshaling the evidence that tends to show that the araucarians and, by implication, the other conifers have had a direct and immediate origin from Cordaitales.

1. GYMNOSPERMS ARE A MONOPHYLETIC GROUP.—There has been a general tendency toward the view that the gymnosperms resemble one another so much more closely than they do any other group that they must therefore have had a monophyletic origin. This point of view was apparently prominent in the minds of more than one (**45, 52, 77**) of the speakers at the Linnaean Society discussion. If the monophyletic origin of gymnosperms be admitted, it follows almost without dispute that they all have had a filicinean origin. Among the known fossil groups of gymnosperms no other can present anything like so strong a claim to be the ancestors of the conifers as the Cordaitales. Just how numerous, striking, and significant are the resemblances between Cordaitales and Coniferales (more particularly Araucarineae) can be best shown by a brief review.

Ever since JEFFREY'S (**27, 28, 29**) division of vascular plants into Lycopsida and Pteropsida on the basis of the presence or absence of

leaf gaps, there has been a very general disposition to accept this distinction as entirely valid so far as it concerns the Pteropsida. Striking as is this fact in the other groups of the Pteropsida, it is preeminently so among the conifers, a small-leaved group where it is not only present in the mature stem but also in the seedling and reproductive axes (31). It is true (61) that the cladosiphonic exarch stems of the ancient lycopods did occasionally become medullated, and it is possible that in the course of evolution some member might have lost all of its centripetal wood, and have developed centrifugal wood and leaf gaps, but there is no evidence as yet that any of them ever actually did either.

The histological structure of the stem is only less strikingly uniform among gymnosperms than the general organization. In fact, the wood of araucarians and cordaiteans is so nearly identical that no absolutely trustworthy tests have yet been discovered for distinguishing them. Although the other gymnosperms do not all have exactly the same arrangement of the bordered pits, they do all have such pits on the radial walls of the tracheids, and they are, on the contrary, with a single exception (48, 53), unknown among the lycopods. While there is greater diversity in the phloem, perhaps that of lycopods differs still more widely.

Aside from the Araucarineae, the structure of the ovulate cones is more readily brought in line with a filicinean than a lycopodinean ancestry. Though the ovulate cone readily lends itself to the derivation of araucarians from lycopods, it can nevertheless be explained in terms of the Cordaitales; while, on the contrary, it is very difficult to explain the cone of a pine in terms of a lycopod ancestry, and next to impossible to so explain those of cycads.

The structure of the seed is remarkably uniform through the entire phylum, from the oldest to the living representatives. Very few lycopods (3, 51, 53) are known to have borne seeds of any kind and even those are much simpler than those of any gymnosperms. I have elsewhere (7) pointed out that these seeds do offer us an analogy of the way in which the peculiar pollination processes of the araucarians may have originated. It may be objected, however, and I think rightly, that if lycopods had developed high grade seeds, they would have been likely to parallel the structures

present in the Pteropsida. Still it remains true that they are not known actually to have done so.

There are no microsporangiate structures known among lycopods that are at all comparable with the pollen cones of the gymnosperms. Notwithstanding the puzzling diversity within the group, it is still far easier to derive them from filicinean ancestors than from club mosses. In the latter the sporangia are uniformly single and adaxial instead of multiple and abaxial, as they are in ferns and gymnosperms.

With the exception of the Gnetales, the female gametophyte of the gymnosperms is so uniform in mature structure and in development as almost of itself to preclude any question of its diverse origin. The deep-seated megaspore, the vacuolated free nucleate embryo sac, the centripetal growth of walled tissue, the origin and development of remarkably uniform archegonia are common to all known members of the group, and form a unique and characteristic series unknown outside of it.

The development and mature form of the embryo, with its free nuclear phase, organization into a walled proembryo, elongating suspensors, and terminal embryo, are no less striking and equally without analogy outside the group. Nor is there any sufficient diversity in the mature structure or in the course of development of the male gametophytes to cast serious suspicion on their common origin. The differences are strictly of degree, and find a ready explanation in the changes incident to a long course of evolution.

As a result, it seems to the reviewer that all gymnosperms resemble one another in very many and very significant ways. On the contrary, it is the araucarians alone that present anything more than very slight resemblances to the lycopods, and even here the significant points of resemblance are few and less exact than the numerous ones that relate them to other gymnosperms.

2. THE ARAUCARINEAE RESEMBLE THE CORDAITALES MORE CLOSELY THAN ANY OTHER CONIFERS.—Among those who hold this view no one has expressed himself more clearly or strongly than SCOTT, who says: "The Araucarineae present a close agreement with the Cordaiteae in the structure of the stem, and particularly in that of the wood, which, as universally admitted, is often indis-

tinguishable in the two families. The essential feature is that the mass of the wood, apart from the medullary rays, is composed of tracheids with multiseriate bordered pits on their radial walls" (**53**, p. 654).

The more recent and comprehensive argument for this view is that of THOMSON (**70**). His arguments may be summarized under four heads: (1) the Araucarineae closely resemble the Cordaitales in the anatomy of the stem, root, and leaf; (2) they are the oldest known conifers; (3) certain mesozoic forms show a transition from Araucarineae toward Abietineae; (4) vestigial structures in leaf, stem, root, and reproductive axes, some of which indicate (*a*) the origin of araucarians from cordaiteans, and (*b*) others of which indicate the origin of Abietineae from Araucarineae.

Although I have not seen the papers by GOTHAN (**21, 22**), the references to them by other writers, particularly JEFFREY and THOMSON, would indicate that he holds similar views respecting the relationship between the Araucarineae and Abietineae.

Speaking of the pith, THOMSON (**70**) says: "In the variability of the size of the pith, and in the magnitude which it may attain, the Araucarineae are the only forms of the conifers at all comparable to those of the cordaitean alliance."

The root is usually diarch, and the protoxylem points are separated into two forks by the presence of a resin duct, as in the Pineae (**70**); nor "is there any indication of a resin duct in the center of the metaxylem, as in the Abieteae."

There is a very broad transitional zone from the primary to the secondary wood in the stem and particularly so in the cone axis. "In no other group of the conifers is there an approach to this cordaitean condition" (**70**).

There are many resemblances between araucarian and cordaitean leaves. The araucarian-podocarp alliance includes the only conifers with leaves at all comparable in size to those of the cordaiteans. In both, the leaves persist for many years; in both, the leaves are parallel and dichotomously veined, with mesarch collateral bundles and remarkably persistent leaf traces.

Although the pitting of the more ancient araucarians was so nearly identical with that of cordaiteans, it "is much reduced in the

mature (stem) wood, and occurs mainly at the ends of the tracheids" (70) in the living forms. Some cordaiteans show a notable tendency in the same direction. The characteristic paleozoic type of pitting is found only in the primitive regions of the living forms (cones and roots).

A torus is present in the bordered pits of all conifers except araucarians and some podocarps (70). It is very poorly developed, when present at all, in the Araucarineae, and entirely absent in Cycadales, Ginkgoales, Cordaitales, Cycadofilicales, and Filicales.

Miss GERRY (20) has proposed to separate araucarians from other conifers on the ground that they lack bars of Sanio in the radial walls of the tracheids, which are possessed by all others. JEFFREY has gone even farther and held that it is the most certain distinguishing feature in separating fossil araucarians from the abietineans (35). On the contrary, THOMSON holds "that a rudimentary bar of Sanio is present in all Araucarineae" and "that the araucarians are not to be separated from the other conifers because of the lack of a bar of Sanio, but rather that they are to be regarded as the basic forms from which this structure in the other conifers has been derived" (70). I have found no reference to its presence in cordaitean wood, so that its absence or feeble development is another point of similarity.

The absence of resin canals in the wood of both Araucarineae and Cordaitales is a well known and striking resemblance. THOMSON holds it to be primitive in both cases (70). He brings forward much argument to show that resin canals in the pines are primitively solid, and that they have been derived from resin parenchyma, which has in its turn replaced the resinous tracheids characteristic of cordaiteans and araucarians. He concludes that "the origin of the resin tissue of the pine alliance from tracheary elements as in the Araucarineae, and the retention of similar stages in its development, forms what the writer regards as one of the fundamental features of relationship between the two groups."

So far as living araucarians are concerned, the cells of the medullary rays are characteristically thin-walled and unpitted, just as they are in the Cordaitales. There are known several mesozoic forms in which the rays approach the abietinean type.

It is obvious that forms intermediate in character may be interpreted as araucarians that are being modified in the direction of the abietineans (**70**), or as pines that are about to be transformed into araucarians (**32, 34, 35**). It appears (**70**) that the older forms are more like the araucarians, while the later ones resemble the pines more closely. The geological sequence thus appears to be in favor of the origin of pinelike conifers from araucarian ancestors.

Recently evidence (**75**) has been adduced to show that marginal ray tracheids have arisen through a modification of the tracheids of the wood, and not by a transformation of parenchymatous cells. The oldest known forms with ray tracheids do not antedate the Cretaceous. Since the Araucarineae are known with great certainty from the Jurassic and probably from earlier strata, the geological evidence appears to favor the view that thin-walled unpitted ray cells are the primitive type.

The albuminous cells of the phloem have been considered (**13, 65, 75**) homologous with the ray tracheids. Their absence from the Araucarineae, accordingly, has been interpreted (**70**) in the same way.

Annual rings are absent or feebly developed in the Cordaitales and in most Araucarineae, though STOPES (**64**) has recently reported a cretaceous *Araucarioxylon* from New Zealand with very definite growth rings.

Aside from the structure of the seed itself, the ovulate cone of *Araucaria* is nearer to that of the Cordaitales than are those of the Abietineae. The essential feature of the cordaitean cone is that the single seed is borne on an axis standing in the axil of a bract. The seed-bearing axis is not always axillary if one may trust the illustrations (**16**). In some cases the bract appears to be borne on the seed stalk. The seed itself is terminal and erect. The cone of *Araucaria* differs in that the bract and axis are much more intimately associated and in that the ovule is inverted and not terminal. There are at least three obvious interpretations of the cordaitean cone. First, one may suppose the cone to be simple, consisting of an axis covered with branched sporophylls, some of which are sterile and some fertile. Secondly, one may suppose that the cone is compound and that the ovule is borne directly on the branch

axis, which stands in the axil of a bract or leaf, or merely arises directly from the main axis among the bracts but without a fixed relation to any of them. Thirdly, one may apply the theory of CELAKOVSKI (16) of the pine cone to it, and suppose that the seed-bearing axis really represents a branch, in the axil of a bract, so intimately united with a sporophyll, which itself bears the seed, that no traces are left of its complex nature.

Without attempting to review the extensive and well known literature relating to this third theory, the writer is disposed to admit that it offers a reasonable explanation of the cones of the Abietineae. It seems much less probable when applied to the araucarian cone or to the ovulate structures of the podocarps and taxads. The attempt to explain the cordaitean cone according to it would appear to be beset with very many grave difficulties. In the first place, most of the evidence used to support it for the modern forms is here unavailable. In the second place, there is no indication in the cordaitean cone itself of such a union of branch and sporophyll. In the third place, it is hardly to be supposed that if such a process had taken place in the ancestors of the pines, there would be still in the present geological age clear indications of it, and that the paleozoic ancestors would have apparently gone so much farther than their modern representatives as to have made their cone appear even simpler than any of them, including even the apparently simple araucarians. Evolution plays strange tricks, it is true, but it really puts a considerable strain on one's credulity to believe, as I think we must if we accept the theory that araucarians are derived from Cordaiteans *through the Abietineae*, that a complex branch system was reduced to a cone in the paleozoic cordaiteans, showing practically no trace of its complexity, then reverted in the abietinean descendants to a stage where the evidence of complexity is again clear, and finally passed on into the araucarians, where the evidence of complexity is again at least doubtful.

It seems to the writer far simpler to make no such difficult assumptions, but to consider that the cones of *Cordaites* and *Araucaria* are no more complex than they appear to be. In any

case, the cones of the two resemble one another closely in apparent structure, and will probably both be eventually satisfactorily explained in the same way.

The seed of *Araucaria* resembles that of *Cordaites* in having the nucellus free from the integument to a zone below the female gametophyte. It is doubtful whether this is a character of any great consequence, inasmuch as there were seeds of both types known among paleozoic plants. Nevertheless, it remains true that this ancient type is not known in any other modern plants. Cordaitean seeds, so far as yet definitely known, appear to have had pollen chambers in the nucellus. Since the pollen has been found in these chambers, in some cases apparently sealed in, one can only infer that the method of pollination was essentially the same as that of modern Abietineae. In this respect the Araucarineae differ very markedly. To the writer the difference appears so great, and the method of the Cordaitales so much superior, that it is difficult to believe that having been once attained it would ever have been given up (36). If there is any dependence to be placed on the facts that appear to indicate that podocarps have been derived from an araucarian ancestry, it would appear that the tendency of evolutionary selection had been in this case in the other direction. This objection does not appear to be very formidable at present, for we know many more seed genera from impressions than we have plants to assign them to. Moreover, we know the internal structure of very few of them. It is not unreasonable to suppose that the Cordaitales may have borne more than one sort of seed, and that among them may have been some which were pollinated in the araucarian fashion.

When the pollen cones are considered, it is at once evident that the closest resemblances to those of the Cordaitales are found in three rather widely unrelated groups: *Ginkgo*, araucarians, and taxads. Doubtless they have all inherited their resemblances from a common source, though along little related lines. So far as the evidence goes, it constitutes a notable resemblance between the araucarians and cordaiteans, in which the abietineans do not share. The araucarian type, with its free pendent sporangia, has apparently been transformed into the more common conifer type with two

imbedded sporangia in the podocarps. It would appear more probable that this transformation had taken place in several lines of descent than that it had taken place in the supposed *Cordaites-Pinus* line, and had then reversed itself in the supposed *Pinus-Araucaria* line. The only very obvious difference between the microsporophyll of *Araucaria* and *Cordaites* is that the pollen sacs are erect and terminal in the latter and reversed in the former. This is precisely the difference in the ovulate cones.

But little evidence can be gathered from the gametophytes, owing to our ignorance of those of the Cordaitales. In both araucarians and cordaiteans the male gametophyte (**4, 5, 36**) is larger than in other modern conifers. It is uncertain whether the gametophyte of the cordaiteans had a more extensive prothallial tissue, like that of the araucarians (**5, 7**), or a more extensive spermatogenous tissue, like that of certain modern cycads (**36, 42**). If I correctly apprehend the abietinean theory of the descent of araucarians, it involves the assumptions that the original male gametophyte possessed a more or less extensive prothallial tissue and at least one antheridium; that in the course of evolution it lost its prothallial tissue with the exception of two primary cells, but retained the spermatogenous tissue of the antheridium (this would perhaps represent the cordaitean stage); that it further lost all of its spermatogenous tissue during its evolution into the Abietineae, except that part giving rise to two male cells; and, finally, that in the course of the evolution of an abietinean into an araucarian the place of pollen deposition became shifted (for reasons not stated) to a point much farther away from the female gametophyte, thereby necessitating the production of a more extensive prothallial tissue (**36**) to supply the needs of the larger amount of cytoplasm required to fill the more extensive pollen tube. Such a course of evolution is presumably possible, though I am inclined to think that the evidence favoring it is yet very inadequate. In the present state of our knowledge the large size of the gametophytes is a point of resemblance between araucarians and cordaiteans, while the pine type of male gametophyte can be easily derived in the same manner from either by the reduction of either or both the prothallial or spermatogenous tissue.

Not enough is known about female gametophytes to make a comparison of much value. The cordaiteans apparently possessed apical archegonia in the manner of all modern conifers. A comparison of embryos of course is at present impossible.

3. THE ARAUCARINEAE ARE VERY ANCIENT PLANTS.—Although wood of the *Araucarioxylon* type is known from the Paleozoic to the present, it is not yet possible to say with certainty just how old are plants corresponding in other essential points with modern araucarians. SEWARD and FORD (**54**) have given us a very careful review of the fossils that have been assigned to the araucarians, to which SCOTT (**53**) has given general agreement. It appears probable, though not beyond question, that such genera of the Permo-Carboniferous as *Walchia* and *Voltzia* were more nearly allied to araucarians than to any other known conifers (**54**). *Voltzia* and *Ullmannia* appear very probable triassic representatives (**24**). There is abundant evidence of impressions, cones, and wood of araucarians in the Jurassic and Cretaceous (**53, 54**).

The Abietineae have been said to extend to the Paleozoic (**33**), and this assertion has been vigorously disputed. The carboniferous form has been discredited on the ground that its source is not known to be from rocks of that age (**21, 22**). The form from the Permian is said by THOMSON and ALLIN not to be a *Pityoxylon* at all, but a cordaitean or *Araucarioxylon*. PENHALLOW appears to have originally regarded it as a *Pityoxylon* on account of what he supposed were horizontal resin canals (**46**). These are now (**71**) said, on a reexamination, not to be resin canals at all, but leaf traces. If these forms are rejected, no true Abietineae are known that can be compared in age with the araucarians.

4. TRANSITIONAL FOSSIL FORMS.—Of late there have been described (particularly by JEFFREY) a number of mesozoic plants with wood more or less intermediate between the true *Araucarioxylon* and abietinean wood. As will be shown in a subsequent section, the JEFFREY school interprets these as evidence of the origin of araucarians from the Abietineae. THOMSON (**70**), however, points out that the earliest of these transitional forms, *Woodworthia* (**38**), is much more like true *Araucarioxyla* than the later ones (as *Araucariopitys*), while the latter are much more

abietinean. He refers particularly to the absence of resin canals, even of the revival type, in the former, and their presence in the latter. The rays of the latter are thick and pitted in the fashion of the Abietineae, while those of the former are thin and resemble those of modern araucarians as well as cordaiteans. In like manner the pitting of the former is more extensive, more crowded and flattened, and with the pits mostly alternately arranged; whereas in the latter they are less numerous, more restricted to the ends of the tracheids, less crowded, and more frequently opposite. He contends that this is consistent either with a cordaitean or an araucarian ancestry for the pines, but difficult to reconcile with an abietinean ancestry of araucarians.

5. VESTIGIAL STRUCTURES, RECAPITULATION, TRAUMATIC REACTIONS.—The broad transitional zone between primary and secondary wood in the araucarian cone has already been mentioned as a remarkable parallel to the condition found in the cordaitean stem. The pitting in the cone is also more extensive. The pits cover the whole radial surface of the tracheids, are crowded and mutually flattened, and there may sometimes be as many as five rows to a tracheid. THOMSON remarks (**70**) that not only does the pitting in the araucarian cone resemble cordaiteans, but that "instead of the opposite pitting, the pitting of the cone axis and early wood of the Abietineae has characteristically either scattered uniseriate pits or biseriate ones which are alternately arranged."

A torus, characteristically present in mature wood of Abietineae and feebly developed in mature wood of Araucarineae, is entirely absent (**70**) in such primitive regions of the latter as cone axis, first-year stem wood, primary and young secondary root wood. They should be expected in some or all of these places if araucarians had descended from abietinean ancestors which possessed them.

Bars of Sanio are well developed in the Abietineae and feebly so in the araucarians (**42, 70**). They are also poorly developed in the primitive regions of Abietineae and in the mesozoic *Pityoxyla*. From this THOMSON infers that well developed bars of Sanio were not characteristic of the ancestors of the pine alliance.

He also argues that, since resin canals are ontogenetically developed from solid parenchyma and are frequently solid in the abie-

tinean cone and in certain fossil forms, resin canals are not actually a character, as JEFFREY maintains (**42**), of the ancestors of modern Abietineae, and much less so of the ancestors of modern araucarians.

The absence of ray tracheids from the seed cone of *Pinus* and of the erect cells of the phloem from the cone and first few years' growth of the stem and root (**13, 70**) is interpreted to mean that these structures have been acquired in the comparatively recent geological history of the group, very probably long since the time at which Araucarineae are supposed to have originated from it.

In the outer extremities of the vascular bundles of the leaf of the Araucarineae there is a considerable amount of centripetal xylem. It has been interpreted in various ways. THOMSON holds that, though much of it is of the transfusion type, there is yet always a certain number of elongated elements that are true centripetal wood lying next the protoxylem (**70**).

Attention has often been called to the fact that seedling pines have only primary needle leaves and only later develop spur shoots. If they are ancestral to araucarians, the latter might be expected to develop spur shoots on the seedling.

Traumatic reactions play little part in THOMSON'S argument, though he does invoke its aid in the attempt to show that the ancestral type of resin canal (**70**) in the pines was solid. He points out that the resin canals produced by wounding modern pines are much more numerous than can reasonably be expected to have been the case in the ancestral forms, and that they are frequently solid. The argument would appear to cut both ways. In a later paper (**73**) he has studied the normal variability of the spur shoot of *Pinus* and has made free use of the effects of wounding to substantiate his conclusions. His general conclusions are that the larger numbers of leaves on the less definite spurs of fossil forms find their counterparts in the normal variations in the number of leaves to a fascicle of living pines, particularly such wide variations as occur frequently on very vigorous branches, on reproductive axes, and on vigorous seedlings. Variation in the number of needle leaves, branching of the spur shoot, the production of primordial leaves on branches, and even on proliferating spur shoots can all

be produced by wounding. He interprets these reactions as a reversion to the ancestral condition as indicated by their occurrence in the fossil forms and in the primitive regions of living forms just mentioned. LLOYD in a recent paper (43) has touched the same subject and given his approval to the general conclusion as stated by THOMSON. The latter calls attention to the fact that the conifers which do not have spur shoots show no evidences, either in their primitive regions or as the result of wounding, that they have descended from ancestors possessing spur shoots.

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